

Brooding patterns in three freshwater mussels of the genus *Elliptio* in the Broad River in South Carolina

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Abstract: We investigated brooding patterns and timing of reproduction in three species of freshwater mussels, *Elliptio complanata* (Lightfoot, 1786), *Elliptio roanokensis* (Lea, 1839), and *Elliptio angustata* (Lea, 1831) in the lower Broad River near Columbia, South Carolina. Through repeatedly marking and recapturing individuals from late March through late June 2008, we determined that *E. complanata* and *E. roanokensis* can complete at least two broods during this season, and that *E. angustata* can complete at least three broods with very little time between broods. The lengths of brooding periods were difficult to estimate and subject to a wide margin of error. However, the brooding period was estimated to be 20 to 36 days in most broods of *E. angustata*, and could be as short as 18 days in *E. roanokensis* and 25 days in *E. complanata*. Mark and recapture of gravid mussels provided a much more detailed picture of brooding strategies than the collection and preservation of different individuals throughout the year.

Key words: *Elliptio complanata*, *Elliptio roanokensis*, *Elliptio angustata*, consecutive reproduction, broods

Freshwater mussels exhibit a wide variety of brooding patterns. Mussels are classified as short-term brooders (tachytictic), in which the female contains developing glochidia for approximately one month, and long-term brooders (bradytictic), in which broods typically last between 8 and 10 months (Ortmann 1912). Detailed literature reviews (Heard 1998, Watters and O'Dee 2000) indicated that although these two classifications have been in use for a long time, a wider variation in reproductive strategies exists. The length of the brooding period may also vary depending upon temperature cues (Watters and O'Dee 2000). In addition to variation in brooding patterns among species, there may be variation among individuals, and among populations in different geographic areas (Heard 1998). Mussels may also brood only once per year (sequential reproduction) or produce more than one brood each year with a minimal time lapse between broods (consecutive reproduction) (Heard 1998).

Brooding patterns, such as the number of broods per year, the season during which mussels brood, and the tendency of mussels to pause or skip a year of reproduction may differ between populations or between years based upon geographic and environmental factors (Hochwald 2001). Understanding responses to these variables may assist

conservation efforts aimed at relieving environmental stresses and increasing reproductive output (Hochwald 2001). Estimating the duration of the brooding season may assist conservationists in regulating activities to minimize disturbance to mussel populations during a particularly sensitive time in their life cycle. Knowledge of the frequency and timing of brooding within a population will also assist researchers in studying evolutionary aspects of a population by estimating fecundity and response to environmental or biological changes. The timing of broods and glochidial release may be especially critical for species that use migratory hosts, or hosts whose activity or feeding behavior varies seasonally. Understanding fecundity, brood production, and brood maturation is also beneficial for propagation programs for rare species.

There are a few documented examples of freshwater mussels that complete 2 broods per year with or without a lengthy rest period in between (Heard 1975, Smith 1978, Parker *et al.* 1984, Jones *et al.* 1986, Gordon and Smith 1990, Watters and O'Dee 2000) although cases in North America are fairly rare. A literature review (Hochwald 2001) indicates that most European species of *Unio* Philipson, 1788 can undergo multiple reproductive cycles within one season.

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We tracked the reproductive status of individual mussels over time and examined the tendency to brood multiple times per season in 3 species in the genus *Elliptio* (Unionidae) Rafinesque, 1819: *Elliptio complanata* (Lightfoot, 1786), *Elliptio roanokensis* (Lea, 1839), and *Elliptio angustata* (Lea, 1831). All of these species are ectobranchous (brooding glochidia in the outer gills only). Hermaphroditism has been known to occur at a low frequency in some populations of *E. complanata* (Matteson 1948, Heard 1979, Downing *et al.* 1989). It is not known whether *E. roanokensis* is monoecious or dioecious, but Van der Schalie (1970) noted that *Elliptio producta* (Conrad, 1836) and *Elliptio dilatata* (Rafinesque 1820), members of the same species complex as *E. angustata*, were occasionally hermaphroditic, but allocated most of their reproductive tissue to one sex. As *Elliptio* species are not sexually dimorphic, it was not possible to determine whether individuals in this study were male, female, or hermaphrodites without removing gonadal tissue.

MATERIALS AND METHODS

Study site

The study site in the lower Broad River in Columbia, South Carolina contained a diverse community of mussels. The site was at the upstream end of a side channel among an island complex that forms the confluence of the Broad and Saluda Rivers, in Richland County (34.00421°N, 81.05748°W). The substrate was composed of sand, gravel, and large boulders. The site was near the fall line and below several small riffles producing a fast current. Previous survey work the year before showed that the area had a diverse and moderately abundant mussel community, containing *Lampsilis radiata* (Gmelin, 1791), *Ligumia nasuta* (Say, 1817), *Strophitus undulatus* (Say, 1817), *Villosa delumbis* (Conrad, 1834), *Unionmerus carolinianus* (Bosc, 1801), *Elliptio complanata*, *Elliptio congaraea* (Lea, 1831), *Elliptio roanokensis*, and *Elliptio angustata*. Only one non-gravid individual of *S. undulatus* was found at the study site. *Unionmerus carolinianus* and *E. congaraea* were also uncommon, and only one and 3 gravid individuals of each species respectively were found at the study site. As *L. radiata*, *L. nasuta*, and *V. delumbis* are bradyctictic, they did not release multiple broods within a season, and their reproductive patterns will be discussed elsewhere.

Field procedures

On 8 days in the summer of 2008, we collected mussels by snorkeling or a combination of scuba diving and snorkeling, depending upon water depth. We opened the mussels by partially prying apart the valves along the ventral margin, and classified them as gravid or not gravid. Gravid was defined as having visible swelling with tubes of glochidia on the outer

gills. On each survey, all non-gravid mussels were etched with a single digit number using a Dremel® tool to indicate the survey date. This allowed us to document the reproductive history of non-gravid mussels should they later be found gravid, while still being able to quickly return them to the river to minimize desiccation and thermal stress. The first time a mussel was found to be gravid, a numbered flexible plastic 4 mm × 8 mm tag (Hallprint Pty Ltd., Victor Harbor, South Australia) was super-glued to the shell. The tag could be used to track the reproductive status of the mussel through time. After all mussels were examined and marked accordingly, they were immediately returned to the river in a small area (roughly 15 m²) that provided suitable habitat but allowed the mussels to be easily relocated. On each successive date, we thoroughly searched this area to recapture mussels in addition to searching a broader area to locate new individuals.

Sampling dates were 27 March, 17 April, 2 May, 14 May, 30 May, 4 June, 17–18 June, and 25 June 2008. On 17 June 2008 a thunderstorm interrupted field work, and the examination and marking of mussels was completed on the following day. Mussels not yet examined were kept in the river in collection bags with wide enough mesh to allow adequate water flow. The start date of sampling was limited by cold water temperatures and high flows, which caused poor visibility and safety concerns for field work. High flows during early April also forced a delay in the second sampling date and a deviation from the desired schedule of sampling at least once every 2 weeks. A decision to conclude the study was made after relatively few gravid individuals were observed on 25 June 2008, indicating that the brooding season was probably nearing its end.

Between 80 and 110 mussels were examined on each date. Recapturing individuals was critical to documenting brooding patterns, and an attempt was made to retrieve as many previously marked individuals as possible. However, retrieving every individual was not always possible, and we tried to achieve a balance between concentrating effort on relocating previously marked individuals and searching for additional individuals of less common species for which reproductive data were lacking.

Multiple broods were determined in individuals found on multiple sampling events and observed to alternate between gravid and not gravid. Because not all mussels were recaptured each time, we present data on the maximum length of the brooding period based only on mussels that were observed on at least three consecutive sampling events and were observed when not gravid, when subsequently gravid, and after brood release.

A Chi-square test compared the tendency of each species to have a second brood. Statistical analysis was conducted in SAS for Windows, version 9.1, SAS Institute, Cary, North Carolina.

Water temperatures

Because temperature can be an important cue in influencing the reproduction of freshwater mussels (Heinricher and Layzer 1999, Watters and O'Dee 2000, Hastie and Young 2003) we report water temperatures for the nearest USGS gauge (USGS 2010) upstream of the study site (Fig. 1). Temperatures downstream are not considered to be similar to those at the study site because of the confluence of another river with a large dam and unusually cold water temperatures. The monitoring station or gauge, USGS site 02160991, is located 41.5 km upstream of the study site, at 34.258333°N, 81.330556°W.

RESULTS

Timing of broods

Elliptio complanata was first gravid beginning on 2 May 2008, and gravid individuals were found continuously through the end of the study on 25 June. Percentages of gravid individuals ranged from 46% on 2 May to 4% on 25 June (Fig. 2A). *Elliptio roanokensis* was gravid on all study dates, and rates of gravid individuals ranged from 35% on 27 March to 3% on both 30 May and 25 June (Fig. 2B). *Elliptio angustata* was also gravid on all study dates, and the frequency of gravid individuals ranged from 56% on 4 June to 8% on 25 June (Fig. 2C).

Number of broods

We observed 14 gravid *Elliptio complanata* out of 36 individuals captured and marked throughout the season. Through multiple recaptures, we confirmed the occurrence of a second brood in 2 of these individuals. If an individual was gravid twice, we needed to recapture it at least twice following the release of the first brood to document the

second brood, and even so, the second brood may or may not have been observed, depending upon the dates of capture versus the dates of the brood. Of the 12 individuals in which we observed one brood, only 4 were recaptured at least twice following the release of the brood.

We observed 19 gravid *Elliptio roanokensis* out of 60 individuals captured and marked. Through multiple recaptures, we confirmed a second brood in 3 of these individuals. Individuals of *E. roanokensis* were more likely to be recaptured than either *Elliptio complanata* or *Elliptio angustata*, probably due to the larger body size and ease of locating individuals. Of the 16 individuals in which only one brood was observed, only 3 were not recaptured, 2 were recaptured only once, and the remaining 11 individuals were recaptured between 4 and 6 times each. Although it is possible that a very late or very early season brood was missed in these individuals, it is likely that many of the individuals recaptured 4 to 6 times following the release of the first documented brood actually brooded only once.

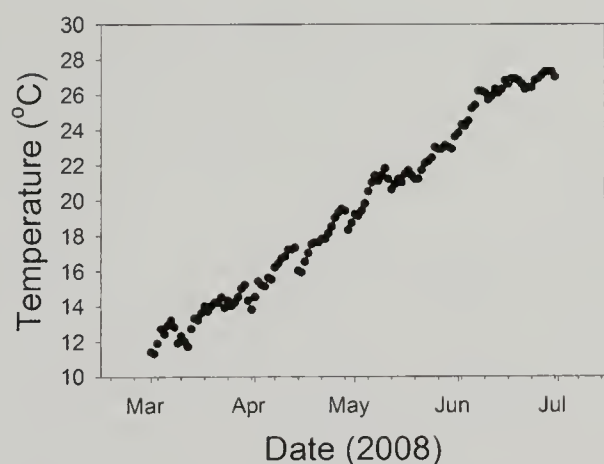


Figure 1. Water temperatures at USGS gauge 02160991, Broad River, near Jenkinsville, South Carolina.

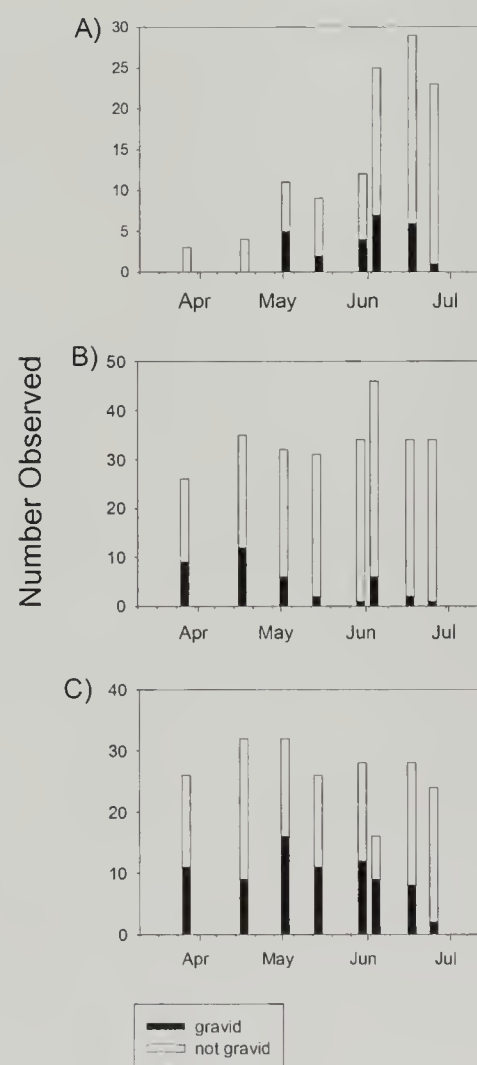


Figure 2. Reproductive status of mussels observed by date: A, *Elliptio complanata*; B, *Elliptio roanokensis*; and C, *Elliptio angustata*. Major tick marks indicate the first day of the month labeled in 2008.

We observed 32 gravid *Elliptio angustata* out of 77 individuals captured and marked during the study. Multiple broods were documented in 8 individuals—4 with 2 broods and 4 with 3 broods. Twenty-four individuals were documented with only one brood. Of these, 15 were not recaptured alive after releasing the first brood, including 3 that were later found dead, as empty relic shells. Three were recaptured only once, 5 were recaptured twice, and one was recaptured 3 times. Of individuals that were observed gravid at least once, all but one of them was captured at least 5 times, and all individuals captured at least 7 times were documented with at least 2 broods, indicating that multiple broods may be more common than a single brood per season. For individuals captured a minimum of 5 times, *E. angustata* was significantly more likely (8 out of 9) than *Elliptio roanokensis* (3 out of 14) to be observed carrying a second brood (Chi-square test, $\chi^2 = 9.99$, $df = 1$, $P = 0.0016$). Only 3 *Elliptio complanata* were captured at least 5 times, which is not enough for inclusion in this analysis.

Length of time between broods

All 3 species were able to begin the second brood fairly quickly after release of the first brood. Of the 2 *Elliptio complanata* observed with 2 broods, the range of possible times between broods were 1 to 20 days and 1 to 29 days. Of the 3 *Elliptio roanokensis* observed with 2 broods, the range of possible times between broods were 29 to 47 days, 1 to 27 days, and 1 to 35 days.

Of the 8 *Elliptio angustata* that were observed with 2 or more broods, the minimum possible time between the first and second brood (since the status of the mussel between capture times was unknown) ranged from 1 to 29 days (mean = 10.25 ± 10.72 SD). The maximum possible time between these broods ranged from 26 to 61 days (mean = 39.75 ± 11.17). For the 4 individuals observed carrying a third brood, the time between broods appeared to be even shorter. All 4 individuals observed carrying a third brood were recaptured only once between the second and third brood, making the minimum possible time between broods always equal to one day. The maximum time between broods was either 17 days (one individual) or 20 days (3 individuals). The apparently shorter interval in individuals observed carrying 3 as opposed to 2 broods may be an artifact of sampling rather than an actual tendency of the second and third broods to be closer in time than the first and second. Individuals that experience the shortest time lapse of any individuals in the population between broods are more likely to be observed with three broods.

Length of brooding period

We calculated a minimum possible brooding period for 9 broods in *Elliptio complanata* that were collected at least

twice in the gravid state without being collected in the non-gravid state in between. Minimum brooding periods ranged from 6 to 16 days (mean = 11.9, SD = 4.0, median = 14). A maximum possible brood length could be estimated only for 3 individuals, because many were not recaptured after the last time they were found to be gravid. The maximum brooding periods were 25, 33, and 42 days.

We determined a minimum brooding period for 9 broods in *Elliptio roanokensis*. Seven of these were individuals that were gravid for a minimum of 17 days, and one was gravid for at least 15 days. The remaining individual was gravid on surveys 55 days apart without being recaptured in between, so this observation was considered an outlier, possibly representing two separate broods. The maximum brood length could only be estimated for 5 individuals since the greatest number of individuals that were gravid was the first day of the study (Fig. 2) and it was not known how long these were already gravid. Maximum brood estimates were 18, 24, 26, 34, and 42 days.

A minimum possible brooding period was determined for 17 *Elliptio angustata*. In one individual, the brood appeared to be in the very early stage during one of the later gravid recaptures. Since this probably indicates that 2 broods occurred during the time these mussels were collected and classified as gravid, this individual was excluded from estimates of brood duration. Minimum potential brood lengths ranged from 6 to 48 days (mean = 23.5 ± 11.7). The 48 day minimum brood appeared to be an outlier, and the next longest estimate of a minimum brood was 36 days. We were able to calculate maximum brood lengths for 10 individuals that were captured as not gravid, later gravid, and non gravid even later, so that the individual was determined to be gravid no longer than the intervening days between non-gravid captures. Maximum potential brood duration ranged from 17 to 62 days (mean = 37.8 ± 17.4 days). Though the possibility exists that some of the broods that appeared to be the shortest were prematurely aborted broods, and some that appeared to be particularly long could have actually been 2 broods, the estimate that broods generally ranged in length from 20 to 36 days would allow 16 out of 17 estimates of minimum brood length and 9 out of 10 estimates of maximum brood length to fall within this range.

Sizes of brooding individuals

Elliptio complanata ranged from 39 to 95 mm in length. Gravid individuals ranged from 61 to 89 mm. *Elliptio roanokensis* ranged from 48 to 141 mm in length, and gravid individuals were from 65 to 130 mm in length. The 65 mm individual was unusual and may have been an error or a misidentified *E. complanata* because the next smallest gravid *E. roanokensis* was 88 mm in length. *Elliptio complanata* and *E. roanokensis* are difficult to distinguish when small. *Elliptio*

angustata ranged from 44 to 104 mm in length. Gravid individuals ranged from 53 to 104 mm in length.

Water temperatures

Average daily water temperatures were 14.5 °C at the start of the study (Fig. 1) when numerous *Elliptio angustata* and *Elliptio roanokensis* were already gravid. Average daily water temperature was 19.1 °C on 2 May 2008 when *Elliptio complanata* was first gravid and 17.0 °C on 17 April 2008, the last day that no gravid individuals were found (Fig. 1).

DISCUSSION

Elliptio complanata and *Elliptio roanokensis* were able to complete at least 2 broods in a season, and *Elliptio angustata* was able to complete at least 3 broods. Three is a minimum number, and we may not have been able to detect additional broods, even if they did occur. For example, with only 8 sampling dates, the maximum number of broods that could be detected is 4, and if 4 did occur during the sampling period, they would be detectable only in individuals recaptured at least 7 times on dates that coincided with alternating gravid and non-gravid periods. Because many gravid *E. roanokensis* and *E. angustata* were collected on the first sampling date, it is unknown how early the brooding season started, and additional broods may have occurred prior to sampling. We appear to have documented the beginning of the brooding season for *E. complanata* because no gravid individuals were found prior to 2 May 2008. Very few individuals were found prior to 2 May (only 3 on 27 March and 4 on 17 April), and it could be that none were found gravid by chance. However, *E. complanata* may migrate below the substrate surface in winter, and emerge at the surface during peak periods of reproductive activity in the spring (Amyot and Downing 1991, Balfour and Smock 1995). Therefore, it is likely that individuals that could not be located occurred below the surface and were not yet reproducing. The low numbers of *E. complanata* early in the study resulted in low recapture rates and little information on the number of broods for this species.

Many studies on brooding patterns in freshwater mussels (reviewed in Bauer and Wächtler 2001 and in Heard 1998) involved sacrificing individuals at periodic intervals, tracking patterns on the population rather than individual level. This can make it difficult to determine the length of the brooding period or whether multiple broods occur. One of the few studies that did track individuals involved the European species *Unio crassus* Philipsson, 1788 in which multiple broods were observed in individuals by checking their reproductive status weekly (Hochwald 2001). More frequent examination of marked mussels would have given us a more accurate picture of brooding patterns but also might have

disrupted reproductive behavior and increased the possibility of injury. However, our methodology clearly documented that some individuals undergo multiple broods in one season and illustrated the benefits of using mark-recapture techniques in reproductive studies.

There appeared to be variation in the number of broods produced by an individual in *Elliptio roanokensis*. While there is a possibility that some individuals observed with one brood actually produced more that were not observed, *E. roanokensis* individuals were frequently recaptured many times following the release of a brood and only a few of those were observed with a second brood. The larger body size of *E. roanokensis* may have again made it easier to locate than smaller species. *Elliptio angustata* may have been more consistent in the number of broods produced since most individuals recaptured at least five times had at least two broods. Not enough data were available to draw conclusions about the prevalence of multiple broods in *Elliptio complanata*. Although little information on variation in brooding patterns among individuals in a single population is available, Hochwald (2001) found that the number of broods per season in *Unio crassus* ranged from 1 to 5. Geographic variation in brooding patterns has also been documented in several species including *E. complanata* (Heard 1998). In most cases, the variation was latitudinal, involving a greater number of broods, longer brooding season, or longer brooding periods in warmer climates. However, exceptions sometimes occur when a population in the middle of the species range exhibits an atypical pattern (Heard 1998).

Elliptio complanata is a relatively well-studied, wide-ranging species. Fertilization and the start of the brooding period takes place from late April to May in Michigan (Matteson 1948) and Wisconsin (Baker 1928), slightly earlier than we observed gravid individuals (May 2). However, our sampling interval of two weeks did not allow us to pinpoint a start of the brooding season later than April 17 but earlier than May 2. Also, our sample sizes earlier in the season were low. Although one would expect an earlier start to the reproductive season in a more southern and warmer river, year to year variation is known to occur in reproductive timing within a population (Matteson 1948, Heard 1998). Perhaps *E. complanata* reproduced later in 2008 than was typical.

The duration of the study did not permit investigation of a second brooding season in the fall. Autumnal brooding has been documented in several North American mussels, but most *Elliptio* species appear to brood in one continuous season in the spring and early summer, or the winter in some tropical areas (Heard 1998). Our data on the length of the brooding period were consistent with the generalization that tachytictic species brood for about one month. However, many individuals, particularly *Elliptio angustata*, completed a brood in a much shorter time frame.

Freshwater mussels clearly exhibit a variety of life history strategies, including variable brood lengths and numbers of broods. Much more data on a wider range of species and populations are needed to investigate geographic variation in brooding patterns within species and selection pressure for various reproductive strategies. We hope that our research will encourage investigators to take a more detailed approach to investigating life history strategies and incorporate mark-recapture techniques. This study had limitations imposed by occasional high water conditions that limited sampling and by relatively low abundance of most species. Mark-recapture sampling could be even more useful in gathering detailed life history data in densely populated areas in frequently sampled smaller streams.

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